孤雌生殖长角血蜱的哈氏器超微结构与发育

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摘要:为阐明长角血蜱 Haemaphysalis longicomis 孤雌生殖种群的哈氏器结构及发育特征,用扫描电镜对其各虫期哈氏器进行了观察,分析了血餐对哈氏器发育的影响。结果表明:该种群幼蜱、若蜱和成蜱哈氏器形态结构基本相同,均由前窝和后囊构成。幼蜱前窝感毛6根,位于同一基盘;若蜱和成蜱哈氏器相似,前窝感毛7根,其中1根孔毛位于外侧基盘,另6根感毛位于内侧基盘。各虫期饱血后哈氏器大小均比饥饿状态下显著增大(P < 0.05)。幼蜱前窝与后囊面积比值与若蜱相比无显著差异(P > 0.05),若蜱前窝与后囊面积比值与成蜱相比差异显著(P < 0.05)。各虫期哈氏器均在发育,且血餐对哈氏器发育有重要影响。幼蜱至若蜱期哈氏器前窝与后囊的发育速度相似,若蜱至成蜱期哈氏器前窝发育快于后囊。本研究结果在一定程度上揭示了孤雌生殖长角血蜱的哈氏器发育规律。

关键词:长角血蜱;孤雌生殖;哈氏器;超微结构;发育;扫描电镜

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Ultrastructure and development of the Haller's organ of parthenogenetic *Haemaphysalis longicornis* (Acari: Ixodidae)

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Abstract: In order to illustrate the structure of Haller's organ and its development in parthenogenetic Haemaphysalis longicornis, the Haller's organ of ticks from the parthenogenetic population of H. longicornis during different developmental stages (larval, nymphal, and adult stages) was investigated with scanning electron microscopy and the effect of blood feeding on the development of Haller's organ was also analyzed. The results showed that there was no essential difference in Haller's organ of all three developmental stages, which is composed of an anterior pit and a capsule. The Haller's organ contains six sensilla located on the same basal disc in the larva. However, it contains seven sensilla in the nymphal and adult stages. A pored sensillum is located on later-basal disc and other six sensilla are located on the basal disc. The Haller's organ of the adult was similar to that of the nymph. The area of the Haller's organ was significantly bigger in engorged individuals than that in unfed ones (P < 0.05) during the larval, nymphal and adult stages. The ratio of the anterior pit's area to the capsule's has no significant difference between the larval stage and nymphal stage (P > 0.05), while has a significant difference between the adult stage and nymphal stage (P < 0.05). The development of Haller's organ occurs in all three stages of the tick and is affected by the blood feeding. The results also indicated that the development of the anterior pit is as fast as the capsule from the larval stage to the nymphal stage, while the development of the anterior pit is faster than the capsule from the nymphal stage to the adult stage. The results partly reveal the development law of the Haller's organ in H. longicornis.

Key words: Haemaphysalis longicornis; pathenogenetic; Haller's organ; ultrastructure; development; scanning electron microscope

蜱类哈氏器位于虫体第一对足跗节背面,由前 窝和后囊构成,是蜱重要的嗅觉感受器(常崇艳等, 1989)。蜱通过哈氏器感受宿主的呼吸、气味及同类的性信息素等(Bruyne and Guerin, 1994; Guerin

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et al., 2000)。Soares 和 Borges (2012)将蜱性信息素和宿主气味提取物作用于哈氏器后在蜱体内检测到电生理信号。因此,哈氏器对蜱类的交配、集群、寻找宿主、躲避危害等起重要作用(李冠民等,1992)。此外,哈氏器超微结构可作为硬蜱分类的依据之一,为硬蜱亚种和亲缘种的分类鉴定提供依据 (Hoogstraal et al., 1968; Homsher and Sonenshine, 1975; 杨银书等, 1992)。

长角血蜱 Haemaphysalis longicornis 广泛分布于 中国、韩国、日本、新西兰等地(Tsunoda and Mori, 2000),是日本立克次体 Rickettsia japonica、卵圆巴 贝斯虫 Babesia ovata、吉氏巴贝西虫 Babesia gibsoni 等多种病原体的传播媒介(白启等,1996; Jongejan and Uilenberg, 2004; Luo et al., 2005), 对人类健康 及畜牧业发展造成极大危害(Estrada-Pena and Jongejan, 1999)。2009 - 2010 年, 在我国河南、湖 北等地相继发生了蜱叮咬后致人死亡的事件,并发 现一株蜱传播的新布尼亚病毒 Bunyavirus, 长角血 蜱可能是该病毒的传播媒介(Yu et al., 2010)。因 此,对其研究具有重要的医学和流行病学意义。本 实验室在四川省苍溪县发现长角血蜱孤雌生殖种 群,并在实验室成功建立其种群。目前,有关长角 血蜱两性生殖种群的形态特征、生物学特性等研究 较多(李晓明等, 2008; 王晓娟等, 2010; Zheng et al., 2011, 2012; Chen et al., 2012), 而对其孤雌生 殖种群研究甚少。周金林等(2004)和李知新等 (2007)分别对上海和甘肃地区长角血蜱孤雌生殖 种群的生物学特性进行了研究, 杨彩明等(2007)对 四川野生动物园长角血蜱孤雌生殖种群各虫期进行 了形态学观察,而有关孤雌生殖种群的哈氏器结构 与发育及血餐的影响未见报道。

本文用扫描电镜对长角血蜱孤雌生殖种群不同 虫期哈氏器进行了观察,详细描述了其形态结构, 分析了血餐对其哈氏器发育的影响。研究结果补充 完善了孤雌生殖长角血蜱的形态学和发育资料,在 一定程度上揭示了孤雌生殖长角血蜱哈氏器发育的 规律。

1 材料与方法

1.1 供试材料

长角血蜱孤雌生殖种群采自四川省苍溪县,在 实验室内进行传代繁殖。非寄生期在实验室光照培 养箱中培养(27 ±1℃, RH 75%, 光周期 6L: 18D)。 寄生期在家兔耳上饱血。随机选取饥饿 3 d 的幼蜱、若蜱和成蜱各 40 头;随机选取饱血的幼蜱、若蜱和成蜱各 40 头,在扫描电镜下观察哈氏器的结构特征。其中饥饿 3 d 的蜱指孵化 3 d 尚未吸血的蜱;饱血的蜱指饱血后自动从兔耳上脱离的蜱。

1.2 扫描电镜观察样品制备

将各虫期的蜱用 2.5% 的戊二醛固定,经酒精脱水,丙酮过夜处理后冷冻干燥。最后喷金,在日立 S-520 型扫描电镜下观察并拍照(Homsher and Sonenshine, 1975)。

1.3 数据统计与分析

采用统计学软件 Statistica 6.0 处理数据,结果以平均值 $\pm SD$ 表示,对各虫期不同营养状态哈氏器大小组间比较用 t 检验,P < 0.05 为差异显著;对不同虫期间哈氏器前窝与后囊面积比值进行方差分析,并用 Newman-Keuls 法对均数间的差异进行显著性检验,P < 0.05 为差异显著。其中,前窝为梯形,前窝横径为梯形的中线,前窝的高为梯形的高,以哈氏器前窝横径和高相乘计算前窝面积;后囊为长方形,后囊的横径为长方形的长,后囊高为长方形的宽,以后囊横径和高相乘计算后囊面积。

2 结果

2.1 长角血蜱幼蜱哈氏器

长角血蜱孤雌生殖种群幼蜱有一对哈氏器,呈长方形,边界模糊。前窝呈梯形,感毛数为6根,位于同一基盘上,其中孔毛1根(表面布满小孔),沟毛2根(表面有长度规则的短沟),细毛2根(表面有不规则的沟),锥毛1根(表面光滑)。后囊呈长方形,囊孔为横缝型,囊内附属物为多形体。哈氏器有3根近端毛(2长1短);有2根远端毛(1长1短),较短的远端毛位于外侧;前窝后囊交界处两侧各有1根侧毛。其形态特征见图版 I (A~C)。饱血幼蜱哈氏器前窝、后囊大小(横径和高)与饥饿幼蜱相比差异显著(P<0.05)(表1)。

2.2 长角血蜱若蜱哈氏器

长角血蜱孤雌生殖种群若蜱有一对哈氏器,呈梨形,边界较清晰。前窝呈梯形,感毛数为7根,其中6根位于内侧基盘上,分别为孔毛1根,沟毛2根,细毛2根,锥毛1根;另1根位于外侧基盘上,为孔毛,弯向内侧。后囊长方形,囊孔为横缝型,囊内附属物为多形体。哈氏器有3根近端毛(2长1短);有2根远端毛(1长1短),较短的远端毛

位于外侧;前窝后囊交界处两侧各有 1 根侧毛。其形态特征见图版 $I(D \sim F)$ 。饱血若蜱哈氏器前窝、后囊大小(横径和高)与饥饿若蜱相比差异显著 (P < 0.05) (表 2)。

2.3 长角血蜱成蜱哈氏器

长角血蜱孤雌生殖种群成蜱有一对哈氏器,呈梨形,边界清晰。前窝形态及感毛数量与分布、后囊形态、哈氏器和刚毛分布和形态、前窝后囊交界处刚毛等均与若蜱相同。其形态特征见图版 I(G

~ I)。饱血成蜱哈氏器前窝、后囊大小(横径和高)与饥饿成蜱相比差异显著(*P* < 0.05)(表 3)。

2.4 长角血蜱不同虫期间哈氏器前窝与后囊面积 比值的变化

幼蜱哈氏器前窝和后囊的面积比为 0.54 ± 0.11 , 若蜱为 0.54 ± 0.07 , 成蜱为 0.63 ± 0.07 。幼蜱哈氏器前窝与后囊面积比值与若蜱的相比无显著差异(P > 0.05); 成蜱哈氏器前窝与后囊面积比值与幼蜱、若蜱的相比差异显著(P < 0.05)(图 1)。

表 1 长角血蜱幼蜱不同吸血阶段哈氏器的形态特征

Table 1 Morphological characters of Haller's organ of Haemaphysalis longicornis larvae during blood feeding

营养期 Nutrition stage	前窝 Anterior pit		后囊 Capsule	
	横径(μm) Width	高(μm) Height	横径(μm) Width	高(μm) Height
饥饿幼蜱 Unfed larva	28.09 ±2.71 b	17.78 ±1.81 b	33.35 ±3.14 b	28.14 ± 3.37 b
饱血幼蜱 Engorged larva	31.57 ±5.14 a	19.37 ± 2.59 a	35.36 ± 2.83 a	30.29 ±1.99 a

各营养期观察蜱数 40 头。表中数据为平均值 $\pm SD$; 同列数据后不同小写字母表示差异显著 (P < 0.05); 下表同。Forty ticks of each nutrition stage were observed for the experimental analysis. Data in the table are mean $\pm SD$, and those in the same column followed by different small letters are significantly different (P < 0.05). The same for the following tables.

表 2 长角血蜱若蜱不同吸血阶段哈氏器的形态特征

Table 2 Morphological characters of Haller's organ of Haemaphysalis longicornis nymphs during blood feeding

++ - V - ++1	前窝 Anterior pit		后囊 Capsule	
营养期 Nutrition stage	横径(μm) Width	高(μm) Height	横径(μm) Width	高(μm) Height
	36.35 ± 2.09 b	32.24 ± 2.61 b	51.86 ± 2.10 b	43.42 ± 3.05 b
饱血若蜱 Engorged nymph	38.05 ± 2.03 a	34.89 ± 2.11 a	52.88 ± 1.97 a	47.13 ± 3.37 a

表 3 长角血蜱成蜱不同吸血阶段哈氏器的形态特征

Table 3 Morphological characters of Haller's organ of Haemaphysalis longicornis adults during blood feeding

营养期 Nutrition stage	前窝 Anterior pit		后囊 Capsule	
	横径(μm) Width	高(μm) Height	横径(μm) Width	高(μm) Height
饥饿成蜱 Unfed adult	62.58 ±5.36 b	61.15 ±4.57 b	86.79 ±4.98 b	70.66 ±4.52 b
饱血成蜱 Engorged adult	67.19 ±4.04 a	64.18 ± 4.87 a	92.51 ±5.02 a	74.05 ±5.27 a

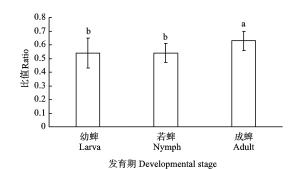


图 1 长角血蜱不同虫期哈氏器前窝与后囊的面积比值 Fig. 1 Ratios of the anterior pit's area to the capsule's area of Haemaphysalis longicornis ticks at different developmental stages 各虫期观察蜱数 80 头,其中饱血状态 40 头,饥饿状态 40 头。柱上方字母表示 3 个虫期哈氏器前窝面积与后囊面积比值的显著性检验结果,不同小写字母分别表示差异显著(P < 0.05,Newman-Keuls检验)。Eighty ticks of each stage were observed,of which forty were unfed and the other forty were engorged. Different letters above bars denote that the ratios of the anterior pit's area to the capsule's area among larval,nymphal and adult stages are significantly different (P < 0.05, Newman-Keuls test).

2.5 长角血蜱哈氏器畸变现象

在240 例样本中发现 4 例畸变哈氏器。其中 3 例为若蜱的哈氏器发生畸变,此哈氏器外侧孔毛从基部分为两枝,呈前后排列,哈氏器内感毛 8 根。另一例为幼蜱的哈氏器发生畸变,其感毛为 5 根,从位置分布推测其缺少一根细毛。其形态特征见图版 I (J, K)。

3 讨论

长角血蜱孤雌生殖种群3个虫期哈氏器的结构 基本相同,均由前窝和后囊构成。孤雌生殖种群幼 蜱哈氏器前窝只有1个基盘,而若蜱、成蜱哈氏器 前窝有2个基盘——内侧基盘和外侧基盘,而内侧 基盘与幼蜱基盘形态和结构相似,表明外侧基盘是 于若蜱期形成的。幼蜱感毛排列方式为6根感毛位 于同一基盘上; 1根孔毛位于其余感毛的远端; 2 根沟毛位于最内侧前后排列;2根细毛基本水平排 列,位于外侧孔毛和远端沟毛之间;锥毛位于外侧 孔毛和沟毛之间,靠近孔毛内侧。若蜱与成蜱的感 毛排列方式为1根孔毛位于外侧基盘上,另1根孔 毛与另5根感毛位于内侧基盘上;其余感毛位置排 列与幼蜱相同。幼蜱孔毛上的孔稀疏, 若蜱较密, 成蜱最密;并且幼蜱孔毛基部有一段无孔区, 若蜱 孔毛的无孔区较幼蜱短, 成蜱孔毛几乎没有无孔 区。幼蜱沟毛表面短沟长度明显大于若蜱, 若蜱沟

毛表面短沟长度大于成蜱。这些可能与哈氏器的功能有关,是长期进化的结果。

各虫期饱血状态下哈氏器均比饥饿状态下显著增大(P<0.05),说明哈氏器在各虫期均在发育,而非仅在某个特定时期发育,且血餐促进哈氏器的发育。幼蜱、若蜱哈氏器前窝与后囊面积比值均为0.54,成蜱为0.63,且幼蜱和若蜱哈氏器前窝与后囊面积比值之间无显著差异(P>0.05);成蜱哈氏器前窝与后囊面积比值和幼蜱、若蜱的差异显著(P<0.05),这说明幼蜱至若蜱时期哈氏器前窝与后囊发育速度相似,而若蜱至成蜱时期哈氏器前窝发育快于后囊。

长角血蜱孤雌生殖种群与两性生殖种群哈氏器结构大体一致,仅缝孔结构有差异。杨银书和李德昌(1991)报道长角血蜱两性生殖种群若蜱哈氏器远端外上方或内上方有一缝孔结构,成蜱哈氏器远端两侧有缝孔结构,而孤雌生殖种群哈氏器未见相似结构。杨银书和李德昌(1991)报道的两性生殖种群哈氏器明显小于本实验观察样本的哈氏器,这可能与孤雌生殖种群独特的繁殖方式有关。

长角血蜱孤雌生殖种群哈氏器结构与其他蜱种相比差异明显。镰形扇头蜱 Rhipicephalus haemaphysaloides 成蜱哈氏器前窝感毛数为6根,后囊7条缝孔,形似"兴"字;草原革蜱 Dermacentor nuttalli 成蜱哈氏器前窝感毛数为6根,后囊1条缝孔,横缝状;亚东璃眼蜱 Hyalomma asiaticum kozlovi 成蜱哈氏器前窝感毛数为6根,后囊7~8条缝孔,放射状(杨银书等,1992)。而长角血蜱孤雌生殖种群成蜱哈氏器前窝感毛数为7根,后囊1条缝孔,横缝状。因此,不同物种哈氏器感毛数量、缝孔形状、基盘数量等存在差异,可作为硬蜱的分类依据之一。

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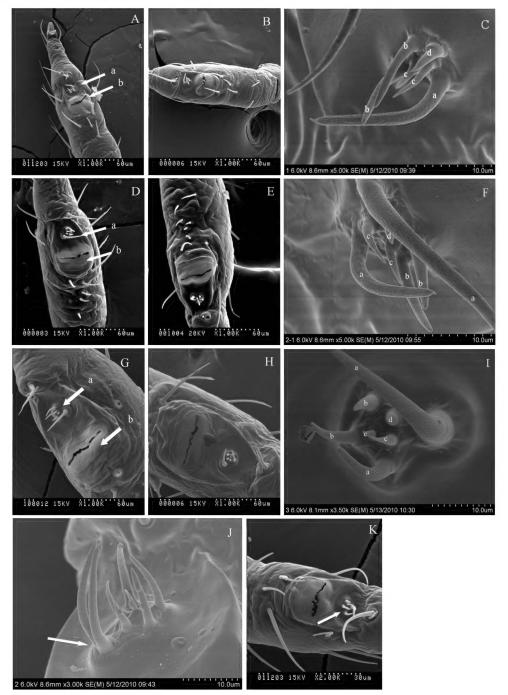
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王多等: 孤雌生殖长角血蜱的哈氏器超微结构与发育 图版 I WANG Duo et al.: Ultrastructure and development of the Haller's organ of parthenogenetic Haemaphysalis longicornis (Acari: Ixodidae) Plate I



孤雌生殖长角血蜱的哈氏器电镜图 SEM micrograph of Haller's organ of parthenogenetic H. longicornis. A: 饥饿幼蜱哈氏器 The Haller's organ of unfed larva (a: 前窝 Anterior pit; b: 后囊 Capsule); B: 饱血幼蝉哈氏器 The Haller's organ of engorged larva; C: 幼蜱前窝感毛 The sensilla of the anterior pit of larva (a: 孔毛 Pored sensillum; b: 沟毛 Grooved sensilla; c: 细毛 Thin sensilla; d: 锥毛 Conical sensillum); D: 饥饿若蜱哈氏器 The Haller's organ of unfed nymph (a: 前窝 Anterior pit; b: 后囊 Capsule); E: 饱血若蜱哈氏器 The Haller's organ of engorged nymph; F: 若蜱前窝感毛 The sensilla of the anterior pit of nymph (a: 孔毛 Pored sensilla; b: 沟毛 Grooved sensilla; c: 细毛 Thin sensilla; d: 锥毛 Conical sensillum); G: 饥饿 成蜱哈氏器 The Haller's organ of unfed adult (a: 前窝 The anterior pit; b: 后囊 The capsule); H: 饱血成蜱哈氏器 The Haller's organ of engorged adult; I: 成蜱前窝感毛 The sensilla of the anterior pit of adult (a: 孔毛 Pored sensilla; b: 沟毛 Grooved sensilla; c: 细毛 Thin sensilla; d: 锥毛 Conical sensillum); J: 若蜱畸变哈氏器,箭头表示畸变处 The aberrant Haller's organ of the nymph, and the arrow showing the location of aberration; K: 幼蜱畸变哈氏器,箭头表示缺失感毛 The aberrant Haller's organ of larva, and the arrow showing the location of the missing thin sensillum.